Pestic. Sci. 1996, 47, 319–325

# Effect of Herbicide Treatment on Host Plant Quality for a Leaf-Eating Beetle

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(Received 22 June 1995; revised version received 30 November 1995; accepted 11 March 1996)

**Abstract:** The effect of sub-lethal chlorsulfuron treatment of the annual weed *Polygonum convolvulus* L. on growth and survival of the folivorous beetle *Gastrophysa polygoni* L. was studied in a controlled environment. Treated and untreated plants were used in whole plant bioassays and in feeding experiments with excised leaves. Direct insect toxicity of the herbicide was studied by use of a Potter Spray Tower. The herbicide was non-toxic to the larvae when applied topically. Larvae fed excised leaves from treated plants did not differ from larvae fed leaves from control plants in terms of developmental time, weight or survival. This suggests that the treatment did not affect the nutritional value of the plant or at least that the beetles could compensate for any such changes. Chlorsulfuron reduced survival of larvae living on whole plants treated with sub-lethal dosages (8 to 67% of the recommended field rate). The mortality of larvae in whole plant experiments was dependent on herbicide dosage and herbivore load. Mortality ranged from approximately 20% on control plants to a maximum of 80% on plants sustaining the highest dosages and herbivore loads. It is argued that the beetles' response to chlorsulfuron-treated plants could be caused by a herbivore-induced plant response enhanced by the action of chlorsulfuron.

Key words: chlorsulfuron, herbicide, induced plant response, insect–plant interaction, *Gastrophysa polygoni*, *Polygonum convolvulus*

## 1 INTRODUCTION

The responses of herbivorous insects to plants treated with sub-lethal dosages of herbicide have only received limited attention (see review by Campbell[1]), although effects on crop plants can increase insect pest populations.[2] Furthermore, herbicides may affect populations of herbivores living on surviving weed plants in treated fields[3] or plants in uncultivated habitats subjected to herbicide deposition.

Many studies of herbicide effects on plant–insect interactions have dealt with phenoxy acid herbicides, including the first observations of increased pest populations due to herbicide application.[4] Nutritional changes of host tissues[5,6] and indirect effects like reduced densities and efficiency of predators[7] or parasitoids[4] have been put forward to explain changes of pest populations following herbicide treatment.

Positive herbivore population responses to sub-lethal herbicide dosages have mainly been found for sap-sucking herbivores[8,9] and insects feeding on meristematic tissues.[4,6] The reason for this may be that sap-sucking insects derive higher nutritional value from their food when the host plant is stressed.[10] Concentrations of free amino acids are consistently found to increase in plants subjected to stressors such as air pollution,[11] herbicide treatment[12] or salinity exposure.[13] The elevated concentration of free amino acids in the phloem probably reflects reallocation of resources from storage tissues to actively growing tissues, resulting in increased assimilate transport in the phloem. However, the nutritional value of whole leaves to folivorous insects does not increase equivalently[14] and therefore defoliators may not derive the same advantage from the stress response as phloem feeders do. Consequently, responses to herbicide treatment may be less straightforward in folivores than in phloem-sucking insects. Folivores have been reported as responding neutrally[15–17] or negatively[3,18] to herbicide treatment of the host plant.

The present study aims to describe how sub-lethal chlorsulfuron treatment of the host plant affects a folivore. Chlorsulfuron is a representative of the sulfonylurea herbicides which are widely used in cereal crops in the western world. The chrysomelid beetle *Gastrophysa polygoni* L. is a common non-target insect in agro-ecosystems where its host plants occur.

## 2 MATERIALS AND METHODS

### 2.1 Plants and insects

*Polygonum convolvulus* L. (Black bindweed) was used for the present studies. *P. convolvulus* is a strict annual weed species. It often climbs adjacent crop plants. Under greenhouse conditions the plant reproduces mainly by self-fertilisation. *P. convolvulus* has no leaf loss during development, but continues to grow until senescence, when all leaves dies almost synchronously and the seeds ripen. Details of the life cycle of *P. convolvulus* are presented by Hume *et al.*[19] Plants for experiments and insect food were grown in pots in a greenhouse. Seeds were harvested and stored cold to break dormancy before sowing.

*Gastrophysa polygoni* L. is a chrysomelid beetle utilizing mainly two food plants *viz. P. convolvulus* and *P. aviculare* L. It eats the foliage of the plants in all three larval instars and as adults. The larvae pupate in the soil. The beetles were kept in culture on *P. convolvulus* plants at 20($\pm$2)°C and 16 h photoperiod.

### 2.2 Whole plant bioassay

A controlled environment experiment was conducted to measure the suitability of chlorsulfuron-sprayed *P. convolvulus* plants as hosts for *G. polygoni*. Eggs of *G. polygoni* were placed on leaves of plants subjected to different herbicide dosages. Plants were sprayed with dilutions of chlorsulfuron 200 g kg$^{-1}$ WG ('Glean' 20 DF; DuPont) at rates corresponding to 0·32, 0·67, 1·32 and 2·68 g AI ha$^{-1}$. The surfactant 'Citowett' (BASF) was added to the spray solutions (5·0 ml litre$^{-1}$). Control plants were treated with water. Treatments were made using a pot sprayer equipped with Hardi 411014 flat-fan nozzles calibrated to deliver 200 litre ha$^{-1}$.

Twenty-eight plants were treated at each dosage. After spraying, the plants were caged singly in polystyrene cylinders and placed in a controlled environment chamber (photoperiod of 16 h, constant temperature of 20°C, relative air humidity of 60% and a photo flux density of 350 $\mu$E m$^{-2}$ s$^{-1}$). Two days after treatment 0, 10, 20 or 40 *G. polygoni* eggs were applied to one or two leaves of the plants. Two leaves were used when 40 eggs were applied. Each treatment was replicated seven times. The eggs were placed on the lower side of leaves in the middle section of the plant according to the behaviour of ovipositing females (unpublished data).

Subsequently, the number of hatched eggs, larvae and adults emerging after pupation was recorded every second or third day. When the adult beetles emerged, they were removed and weighed. Due to the limited size of the controlled environment chamber the experiments were conducted in two parts with 84 plants in each. The data for beetles on control plants were not significantly different in the two trials (paired *t*-test, $P < 0{\cdot}01$), and all the data were pooled.

#### 2.2.1 *Statistical analysis*

One-way ANOVA for unequal sample sizes (i.e. General Linear Models) was carried out to test for effects of herbicide treatment and herbivore load on survival and developmental time. The analysis was run as a Model I ANOVA. If significant effects were found, Tukey *t* tests were done on mean survival and developmental time between treatments.

### 2.3 Intrinsic insect toxicity

First-instar larvae of *G. polygoni* were sprayed with chlorsulfuron in a Potter Spray Tower. First-instar larvae were used because we expected a high susceptibility in this stage due to a high surface/volume ratio and a soft, permeable cuticle. The larvae were treated in batches of 10 with three replications for each rate, i.e. 0 (control), 0·0012, 0·012, 0·12 and 1·2 mg cm$^{-2}$ respectively. The recommended field rate corresponds to $4 \times 10^{-5}$ mg cm$^{-2}$. Mortality was recorded daily. Larvae were supplied with new leaves each day until pupation (six days).

#### 2.3.1 *Statistical analysis*

A one-way Model I ANOVA was used on effects of topical herbicide treatment on the mortality of *G. polygoni*. Data were assumed to conform to a Normal frequency distribution.

### 2.4 Feeding experiments with excised leaves

Feeding experiments were conducted to assess the food quality of chlorsulfuron-treated *P. convolvulus* to *G. polygoni*. Food quality of the host plant was expressed by four parameters describing herbivore vitality, *viz.* fresh weight of the individuals measured regularly during development from egg to adult, the time used to complete larval development, consumption by third-instar larvae and survival until pupation.

Seeds of *P. convolvulus* were germinated and the seedlings were potted and placed in a greenhouse. Plants having four to six leaves were sprayed with either water or chlorsulfuron. Plants were sprayed to the point of run-off with a hand-operated atomizer (for a detailed description see Kjær[20]). The concentration of chlorsulfuron corresponded to 1·6 g AI ha$^{-1}$. Earlier studies

have shown that this chlorsulfuron dosage has significant negative effects on growth rate and reproduction of *P. convolvulus* without killing the plants.[20]

Newly hatched larvae were collected from a laboratory stock. The larvae were second-generation raised. In the experiments, larvae were transferred singly to excised leaves placed in Petri dishes lined with moist paper. New leaves were supplied whenever necessary to maintain a food surplus. For $L_1$ and $L_2$ larvae, new leaves were supplied every second day. $L_3$ larvae had new food every day, because of accumulation of faeces on the surface of the leaf and increased consumption. Leaves were taken from undamaged plants to avoid induced secondary effects of defoliation in food plants. All experiments were conducted at a temperature of 20(±2)°C.

Consumption by third-instar larvae that were fed different leaf types was measured. Leaves abscised from plants were split along the midrib and both halves were transferred to a Petri dish lined with moist filter paper. After 1 h of acclimatization, fresh weight of the leaf parts was measured. One half was then used as food for the larvae. In order to calculate the fw : dw ratio of the specific leaf, the other half was dried for 12 h at 105°C and weighed. Twenty-four hours after application, the larvae were removed, faeces were washed off the leaves and dry weights of the leaves were measured. Consumption of leaf dry matter could then be computed.

Effects of herbicides may appear long after the actual treatment. Therefore, the experiments were carried out 11, 24 and 42 days after spraying of the plants. Eleven days after herbicide treatment, the plants had not produced any new leaves and larvae were therefore only fed leaves which had been directly exposed (type A) and leaves from control plants (type 0). Twenty-four days after treatment, the leaves present at the time of spraying were dark green and very friable and shortly afterwards they died. In this trial the larvae were fed either these leaves (type A), leaves from treated plants produced after herbicide treatment (type B) or leaves from water-treated plants (type 0). Forty-two days after spraying, only leaves produced after the treatment were left. From these plants, larvae were fed leaves produced shortly after treatment (type $B_1$) or newly produced leaves (type $B_2$).

### *2.4.1 Statistical analysis*

One-way ANOVA for unequal sample sizes (i.e. General Linear Models) was carried out to test for effects of herbicide treatment on growth pattern and weight of emerging adults. The analysis was run as a Model I ANOVA. If significant effects were found, Tukey *t* tests were performed on mean survival and development time between treatments. Differences in survival of beetles fed different leaf types were tested by means of binomial tests. The comparison of development time was done by use of paired *t*-test. Finally, the consumption rates were tested with a Mann Whitney U-test, because data were not Normally distributed. Tests of Normal frequency distribution were done by means of Kologomorov–Smirnov One-sample tests.

## 3 RESULTS

### 3.1 Whole plant bioassay

The survival of *G. polygoni* from egg hatch to imago was significantly affected by chlorsulfuron treatment of the host plant (One-way ANOVA, $F = 23{\cdot}3$, df = 4, $P < 0{\cdot}0001$) (Fig. 1). Survival on water-treated plants and on plants treated with the two lowest chlorsulfuron rates (0·32 and 0·67 g AI ha$^{-1}$) were unaffected by the number of insects present on the plant (One-way ANOVA, $F = 1{\cdot}2$, df = 15, $P > 0{\cdot}455$; $F = 2{\cdot}1$, df = 11, $P > 0{\cdot}144$ and $F = 1{\cdot}66$, df = 13, $P > 0{\cdot}301$ respectively), whereas at the two highest chlorsulfuron rates (1·33 and 2·68 g AI ha$^{-1}$) the herbivore density affected survival negatively (One-way ANOVA, $F = 2{\cdot}06$, df = 22, $P < 0{\cdot}047$) (Fig. 2).

Because of the density-dependent herbivore mortality, data were classified in three herbivore density classes according to the number of eggs that hatched on the plant, i.e. 1–12, 13–24 and 25–36 hatched eggs. At the lowest herbivore density 80% of the individuals survived to the adult stage on unsprayed plants; on chlorsulfuron-treated plants the survival decreased significantly with increased herbicide rate up to 0·67 g AI ha$^{-1}$ (Tukey *t*-test, $P < 0{\cdot}05$). At this level survival was 60% and no further decrease was observed. For the two highest herbivore density classes on average 67% (13–24 hatched eggs) and 80% (25–36 hatched eggs) of the larvae survived on unsprayed plants. In both classes a significant reduction in survival

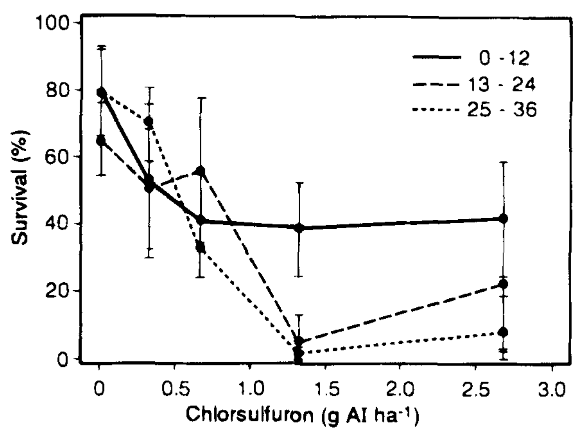


**Fig. 1.** Survival of *Gastrophysa polygoni* on host plants treated with different rates of chlorsulfuron. Survival was registered by counting the number of adults emerging from the soil compared to the number of eggs which hatched on the plant. Data are separated into three classes according to the number of hatched eggs on the plant. Recommended field rate is 4 g AI ha$^{-1}$. Bars represent Standard Error of Mean.

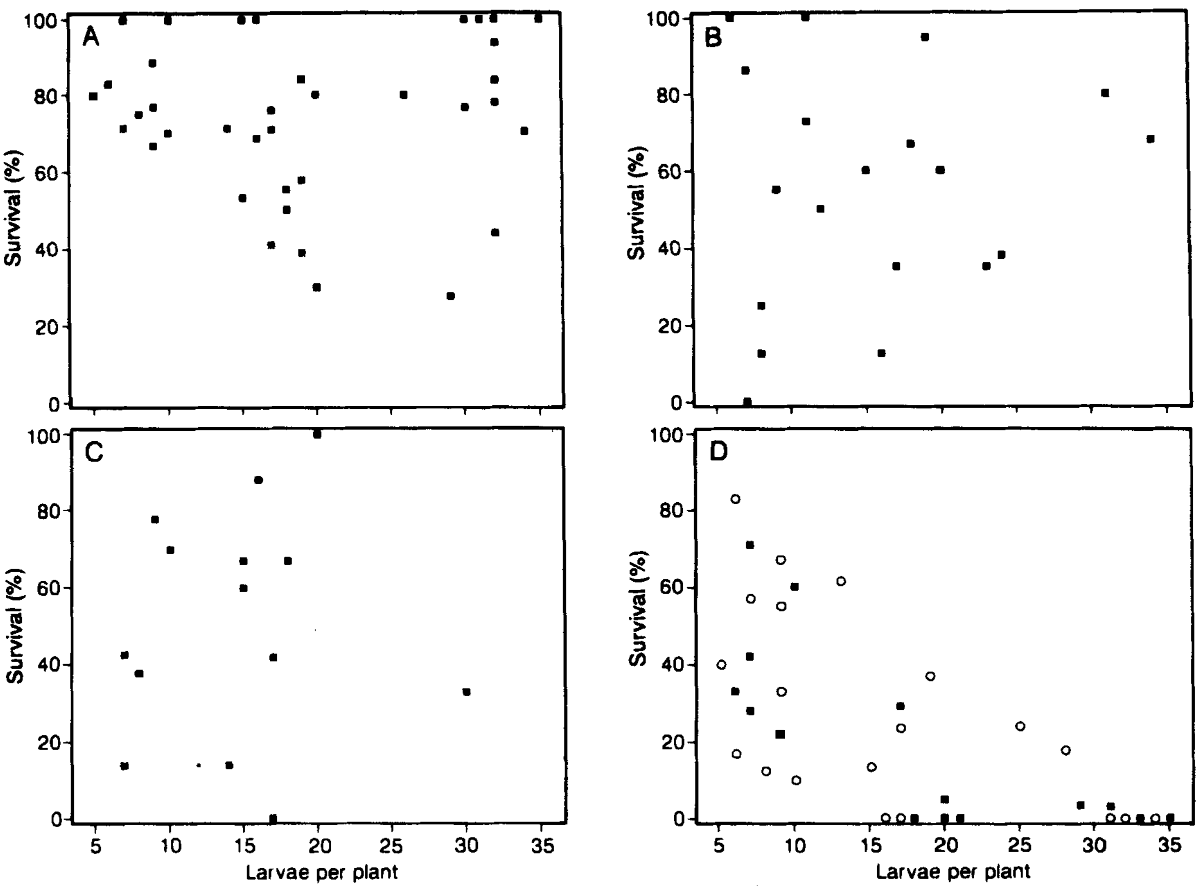


**Fig. 2.** Survival of *Gastrophysa polygoni* from egg to imago on chlorsulfuron-treated *Polygonum convolvulus* plants in relation to herbivore load (number of hatched eggs on the plant). Herbicide dosages (g AI ha$^{-1}$): 0 (Fig. 2A), 0·32 (Fig. 2B), 0·67 (Fig. 2C), 1·32 (■) and 2·68 (○) (Fig. 2D). Recommended field rate is 4 g AI ha$^{-1}$.

was observed as a response to increasing herbicide rates. Above 1·33 g AI ha$^{-1}$ no further decrease of survival was observed (Tukey *t*-test, $P < 0{\cdot}05$). Mortality was mainly observed in the first two instars. The development time from egg hatch to pupation of *G. polygoni* larvae was significantly affected by herbivore load and herbicide rate (One-way ANOVA, df = 21, N = 56, $F = 3{\cdot}12$, $P < 0{\cdot}006$ and df = 2, N = 56, $F = 10{\cdot}38$, $P < 0{\cdot}0007$, respectively). The duration of larval development was 10·1($\pm$0·3; SEM) on control plants. Larvae on plants treated with 0·32 and 0·67 g AI ha$^{-1}$ had a prolonged time of development (paired *t*-test, $P < 0{\cdot}05$). They spent 12·6($\pm$0·7) and 12·4($\pm$0·7) days respectively to reach the adult stage. Development time was not measured for the two highest herbicide rates. The dry weight of the emerging imagoes decreased with increasing chlorsulfuron rates applied to the host plants {Dry weight (mg) = 2·14 − 3·24 × Dose (g AI ha$^{-1}$); r = 0·30, $P < 0{\cdot}0001$, N = 952}.

### 3.2 Intrinsic insect toxicity

No significant changes in the direct mortality rate were found after application of chlorsulfuron to first-instar larvae of *G. polygoni* (*t*-test, $P < 0{\cdot}05$) (Table 1). The highest rate was equivalent to approximately $3 \times 10^4$ times the recommended field rate.

### 3.3 Feeding experiment with excised leaves

The weight of larvae fed treated plants was the same as the weight of those fed on leaves from untreated plants (One-way ANOVA, $F = 1{\cdot}49$, df = 4, $P \geqslant 0{\cdot}203$). Growth patterns of larvae fed leaves from

**TABLE 1**
Survival of First-Instar Larvae of *Gastrophysa polygoni* Topically Treated with Chlorsulfuron in a Potter Spray Tower

| *Rate* (*mg AI cm*$^{-2}$) | *Survival* (%) | *S* *Standard error* |
|---|---|---|
| 0·0 | 0·90 | ±0·10 |
| $1{\cdot}2 \times 10^{-3}$ | 0·80 | ±0·15 |
| $1{\cdot}2 \times 10^{-2}$ | 1·00 | ±0·00 |
| $1{\cdot}2 \times 10^{-1}$ | 1·00 | ±0·00 |
| 1·2 | 0·90 | ±0·06 |

Survival was measured until pupation of the treated larvae (six days). No significant effect was found of treatment (One-way ANOVA, $F = 0{\cdot}95$, df = 4, $P \leq 0{\cdot}47$). Field rate of chlorsulfuron is $4 \times 10^{-5}$ mg AI cm$^{-2}$.

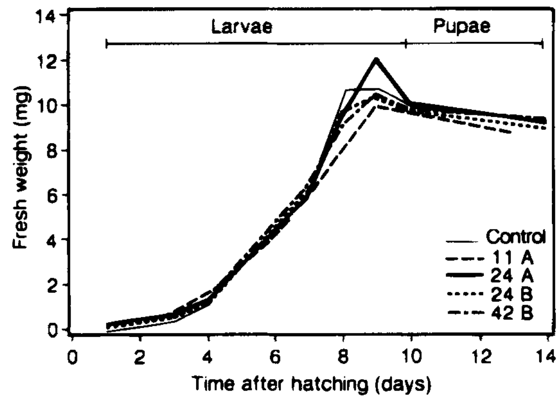


**Fig. 3.** Growth of *Gastrophysa polygoni* from hatch to pupation. The larvae were fed excised leaves from chlorsulfuron-treated host plants (*Polygonum convolvulus*). 11, 24 and 42 is the time (days), after spraying of the plants. A are leaves exposed to direct herbicide spray. B are leaves produced after the spraying. The plants were sprayed with 1·6 g AI $ha^{-1}$.

chlorsulfuron-treated plants at different intervals after herbicide application were not significantly changed (One-way ANOVA, $F = 2{\cdot}28$, df = 3, $P \geqslant 0{\cdot}071$) (Fig. 3). Both survival and development time were unaffected by the treatment of the host plants (paired *t*-test, $P > 0{\cdot}05$) (Table 2). The development times of larvae on excised leaves were not significantly different from those of larvae on intact untreated host plants (paired *t*-test, $P > 0{\cdot}05$). For all treatments, the survival rates were above 80% and not significantly different from each other (binomial test, $P > 0{\cdot}05$) (Table 3).

Consumption by third-instar larvae was unaffected by the herbicide treatment, except when fed leaves very close to dying (24A) (Mann Whitney U-test, $P < 0{\cdot}05$). Larvae feeding on leaf type 24A had a significantly higher consumption rate (Table 3).

## 4 DISCUSSION

Chlorsulfuron was non-toxic to *G. polygoni* when applied directly in a Potter Spray Tower (Table 1), even at dosages many times the recommended field rate. The nutritive value of the host plant was not affected by chlorsulfuron treatment, as feeding on excised leaves from sprayed plants did not significantly affect survival or growth of the herbivore insect compared to excised leaves from unsprayed plants (Table 2). Neither did chlorsulfuron in general affect the consumption rate of larvae. Only when leaves close to dying, due to the combined effects of age and chlorsulfuron exposure, were fed to the larvae, was a significant increase in consumption rate observed (Table 3), but development time was not prolonged (Table 2).

Chlorsulfuron did, however, affect the performance of *G. polygoni* on whole plants by changing the quality of the host, and the effect was dependent on the herbivore density. Host quality was measured as survival, development time and pupal weight. Survival of the beetles decreased with increasing herbicide rate, and development time was prolonged for surviving larvae feeding on whole sprayed plants. Furthermore, dry weight of the pupa was inversely correlated with rate within the applied range.

The results suggest that an induced plant response mechanism exists in *Polygonum convolvulus*, but this mechanism is not effective against larvae on control plants. In these plants, the actual herbivore load may not have been adequate to induce a chemical reaction

**TABLE 2**

Survival and Development Time of *Gastrophysa polygoni* Larvae Fed Leaves from *Polygonum convolvulus* Plants Subjected to Different Rates of Chlorsulfuron

| *Time since spray (days)* | *Rate (g AI $ha^{-1}$)* | *Leaf type* | *N* | *Development time*[a] *(days)* | *Survival*[b] (%) |
|---|---|---|---|---|---|
| 11 | 0·0 | 0 | 20 | 9·3 | 100 |
| | 1·6 | A | 10 | 9·7 | 80 |
| 24 | 0·0 | 0 | 20 | 10·2 | 100 |
| | 1·6 | A | 20 | 10·0 | 95 |
| | 1·6 | B | 20 | 10·2 | 100 |
| 42 | 1·6 | $B_1$ | 20 | 10·8 | 90 |
| | 1·6 | $B_2$ | 20 | 10·0 | 90 |

Leaf type O are leaves of water-treated plants. Type A are leaves exposed to direct herbicide spray. Type B are leaves produced after treatment. $B_1$ are the first new leaves produced after spraying and $B_2$ are leaves produced later.

[a] Test of differences in time used to complete larval development was done by paired *t*-tests. No significant effects were found ($\alpha = 0{\cdot}05$).

[b] Test of differences in survival was done by means of binomial tests. No significant differences were found ($\alpha = 0{\cdot}05$).

**TABLE 3**
Consumption Rate of Third-Instar *Gastrophysa polygoni* Larvae on Foliage of Chlorsulfuron-Treated Host Plants

| | Consumption rate ($g^{-1}$ dry weight $g^{-1}$ fresh larval weight $day^{-1}$) | | | |
|---|---|---|---|---|
| *Days after spraying* | *Leaf type* | | | |
| | *0* | *A* | $B_1$ | $B_2$ |
| 11 | 0·41a | 0·65a | — | — |
| 24 | 0·86a | 1·86b | 0·69a | |
| 42 | — | — | 0·67a | 0·55a |

Experiments were conducted 11, 24 and 42 days after spraying. All plants were treated with 1·6 g $ha^{-1}$. Leaf type 0 are leaves of water-treated plants. Type A are leaves exposed to direct herbicide spray. Type B are leaves produced after treatment. $B_1$ are the first new leaves produced after spraying and $B_2$ are leaves produced later. Significant effects were found where numbers are followed by different letters (Mann–Whitney U-test $P < 0{\cdot}05$).

sufficient to affect a specialized herbivore like *G. polygoni*. Even though not statistically significant, a trend of decreasing survival with increasing herbivore load was observed for insects on control plants (Fig. 2A). It is well known that insect feeding can induce changes in host plants, resulting in decreased food quality (see review by Karban & Myers[21]). Records of herbicides influencing the effect of induced plant responses on herbivorous insects are not known to the authors, but for a number of plant species the range of several secondary plant metabolites is known to be affected by herbicides.[22]

In the present study chlorsulfuron enhanced the effect of induced plant response, because otherwise such induced responses should have occurred equally in both treated and control plants. Other studies have demonstrated that chlorsulfuron increases the concentration of chemicals produced in the leaf because it inhibits the transport (and dilution) of compounds out of the leaf.[23,24] With increasing chlorsulfuron dosage, the inhibition can be expected to increase, thereby increasing the concentration of induced chemicals and the possibility of these chemicals reaching levels toxic to insects. The density-dependent herbivore mortality (Fig. 2) is thought to be caused by herbivore-density-dependent production of these substances in the plant. The lack of effects in the experiment with excised leaves is explained by the low herbivore load used in this experiment (1 per leaf).

Chlorsulfuron has been found to affect the synthesis of allelochemicals in some plants. Suttle *et al.*[25,26] found that chlorsulfuron treatment elicited an increased content of phenolic compounds in sunflower. A similar reaction might be found in *P. convolvulus*. At least one chemical, the flavonoid rutin, extracted from *P. convolvulus*, is capable of deterring, inhibiting or killing insects,[27–29] but further studies are needed to explore the chemical nature of the factor responsible for the increased mortality. The effect of chlorsulfuron on plant–insect interactions is probably rather specific and not applicable to herbicides with different phytotoxic properties.

If the kind of herbicide-induced disturbance of plant–insect interactions described here is significant in the field, it is of importance to agriculture when considering crop plants. It also is of importance to environmental protection in regard to deposition of herbicides on uncultivated vegetation. Moreover the results are of interest to conservation and wild life management when evaluating the value of surviving weed plants after herbicide spraying as basic links in food chains of the agroecosystem, particularly when reduced rates are applied. The results from the laboratory experiments suggests that *P. convolvulus* plants surviving chlorsulfuron treatment are only of limited value as food resource for herbivorous insects, particularly at high herbivore densities. However, in agricultural fields a very possible alternative is no host plants at all.

## ACKNOWLEDGEMENTS

The authors are grateful to Dr Thomas Secher Jensen and Dr Jens Kvist Nielsen for valuable comments on the manuscript, and to The Danish Institute of Plant and Soil Science, Flakkebjerg, for permission to use their spraying equipment. C. Kjær was partly funded by the Danish Research Academy.

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